DROUGHT DAMAGE ON MOUNT TOWRONG, VICTORIA

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(Plate I)

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Synopsis

The vegetation on Mount Towrong in south-central Victoria was severely desiccated in the widespread drought of 1967–68. Severe damage was inflicted on trees and shrubs in woodlands on the hot rocky western slopes and in tall forests along gully margins. A study of the ecotones between the various communities allowed a relative drought resistance ranking of species to be compiled. Amongst the dominants *Casuarina stricta* was the most drought resistant, followed by *Eucalyptus goniocalyx*, *E. radiata* and *E. obliqua*. This order corresponds to their site ranking along moisture gradients in Victoria. Damage was more severe in dense than in open stands.

Studies on the water relations of seedlings of the dominant species confirm this ranking of resistance. Most of the resistance of the species is concerned with drought avoidance and with the efficient reduction of cuticular transpiration. In addition *C. stricta* appears to be more inherently resistant to tissue desiccation and high temperatures. It also develops deep-striking tap roots at an early stage. Seedlings of *E. goniocalyx* and *E. radiata* are closely matched although the former species appears to endure higher tissue dehydration, resists water loss from stems and develops an early robust root system. The adult foliage of *E. radiata* has a lower cuticular control and poorer resistance to desiccation than the juvenile foliage. The development of its seedling tap root is also very slow. *E. obliqua* transpires relatively rapidly and has poor cuticular control of water loss. It is sensitive to tissue dehydration and its tap root development is relatively poor. It is suggested that many of these characteristics may have adaptive value in determining which particular sites the species will occupy. It is likely that the distribution of the species depends not only on the level of average rainfall and soil moisture storage but also on the frequency of extremes.

Description

In 1967 and in the summer of 1968 a drought of unprecedented severity gripped most of Victoria and caused the death or damage of native vegetation, mostly in areas in the 50–100 cm rainfall belt. This followed the 1965 drought in New South Wales and in the Australian Capital Territory which had caused damage to forests on a scale hitherto unknown (Pook *et al.*, 1966). In April 1968, after the drought in Victoria had broken, the western slopes of Mount Towrong looked as though they had been swept by a patchy fire. By the spring of 1968 many drought-damaged trees had developed epicormic and coppice shoots. In the following autumn the field study described in this paper was carried out by senior ecology students of the Botany Department, Melbourne University.

Physiography and Soils

Mount Towrong (800 m) is the highest part of the spur which runs 5 km south-westerly from the Macedon massif on the Great Dividing Range, to a point 1 km east of the Upper Macedon township. The end of the spur rises 150–240 m above Stony Creek on the west and the Gisborne uplands on the east (Pl. I, bottom). The slopes vary from 11° to 25°, depending on the presence of small gullies and more or less resistant rock. The spur, like most of Mount Macedon, consists of well jointed Upper Devonian dacite (Skeats and Summers, 1912) (Fig. 1). Zones of deeper soils carrying forest run diagonally across the western slopes. These are flanked by broad areas of rock outcrops and rocky soils which

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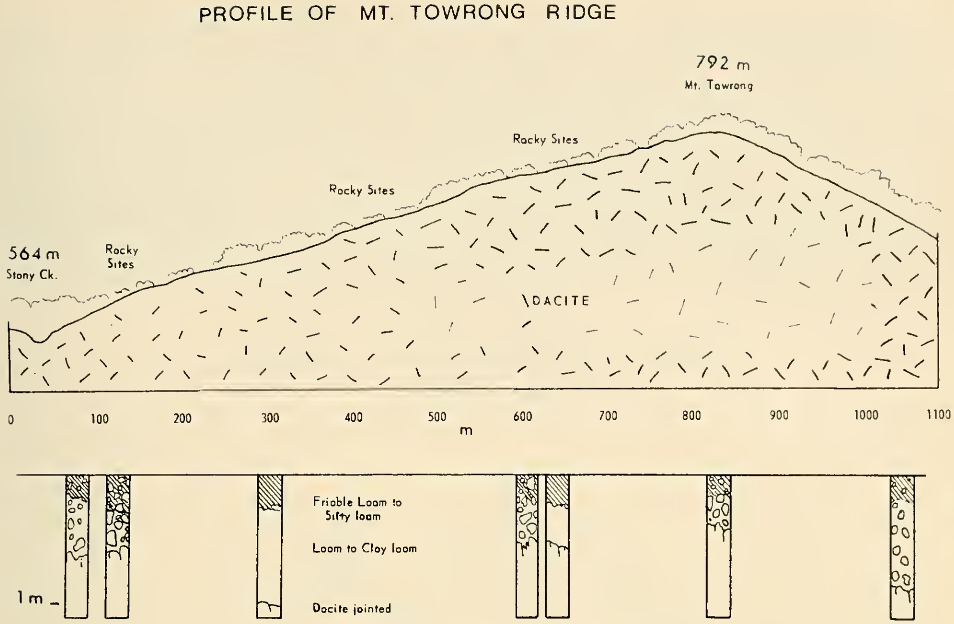

Fig. 1. Profile of Mount Towrong ridge with soil profiles (westerly to easterly).

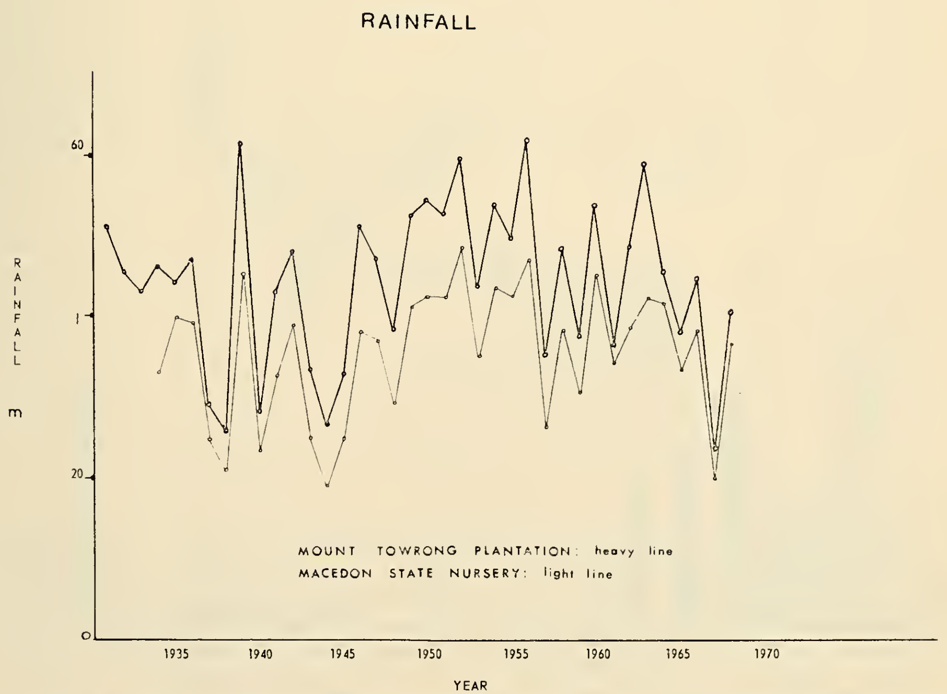

Fig. 2. Annual rainfalls of nearby stations. Mount Towrong 1109 mm and Upper Macedon 846 mm (average).

carry low woodland. The north-south trend of these zones may reflect a major joint system in the dacite. These deeper soils, which are of the krasnozem type, are friable red-brown silty to fine sandy loams increasing in clay content with depth. On the eastern aspect and on the gentler slopes of the mid-western aspects the soils are relatively deep (120–500 cm); elsewhere they are shallow (30–45 cm) with numerous rock floaters 7–30 cm in diameter which become more frequent with depth and merge with the parent rock. The skeletal soils around areas of rock outcrop on the ridge top and close to Stony Creek contain between 20% and 33% rock by volume in the top 30 cm of soil. In other areas rocks are absent in the top soil or the volume is less than 10%. The moisture storage capacity of soil in the top 45 cm ranged between 20% and 25% over most of the area but increased to 35–40% towards Stony Creek.

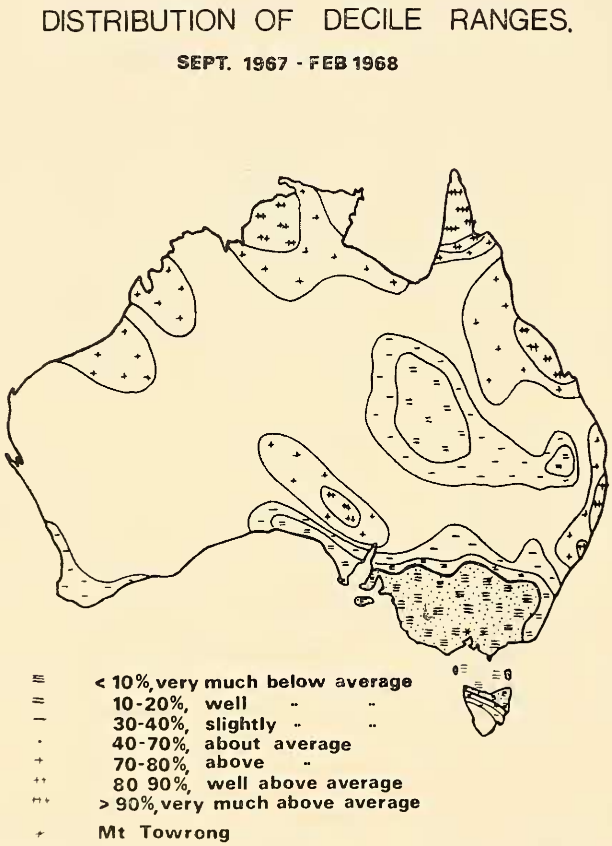

Fig. 3. Decile ranges in Australia during the drought period.

Climate

The climate of the area is normally relatively mild and moist. The rainfall occurs mainly from late autumn to mid-spring and is fairly reliable (Australian Bureau of Meteorology, 1968). The annual rainfall ranges between that at Upper Macedon (84·6 cm at 610 m) to that at the Mount Towrong plantation (110·9 cm at 840 m). At each station the maximum deviation observed over 35 years is about 50% of the mean. In 1967 the rainfall was half of normal and was the same as that of the bad drought years of 1938 and 1944 (Fig. 2). Virtually the whole of the south-east of Australia suffered rainfalls within the lowest 10% frequency of all records. Such a rainfall range has been termed "decile 1" by Gibbs and Maher (1967) and is indicative of severe drought (Fig. 3). The monthly rainfall was consistently low and only the August 1967 rainfall was above average. The spring rains failed badly and the following summer was dry and hot. The drought did not break until April 1968 (Fig. 4). The seasonal distribution of the rainfall and the blisteringly hot winds of February 1968 probably contributed to the severity of the drought symptoms.

Local variations in climate on the Towrong spur are likely to include greater incidence of mist and fog above 600–750 m and, in addition, the westerly slopes are likely to be warmer than the easterly due to the position and altitude of the

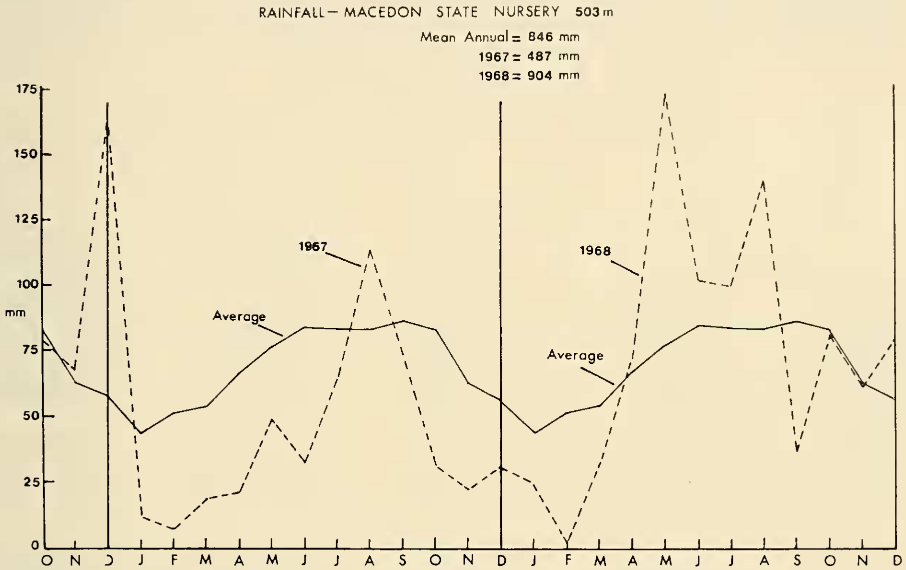

Fig. 4. Seasonal rainfall 1967–68 compared with 30-year mean.

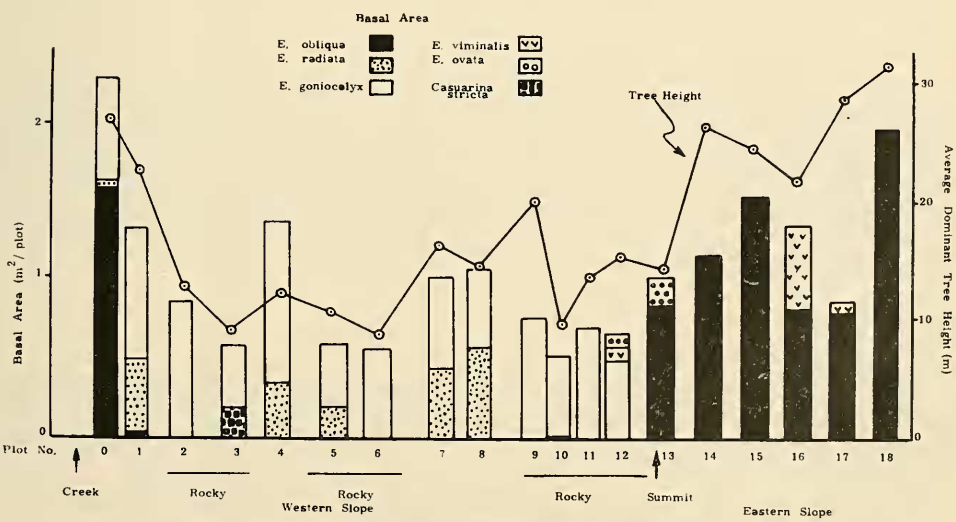

Fig. 5. Basal area and height of eucalypts.

sun in the hottest part of the day. Evaporation is also likely to be greater on the westerly slopes due to the north-west to south-west direction of the prevailing winds.

Method of Study

The vegetation was studied by means of offset plots at 30–90 m intervals along a 900 m transect line from Stony Creek up the west, south-west and west-north-west slopes to the summit, thence down the east-south-east slope. At each site tree heights and girths were measured over 0·022 ha plots (Fig. 5) and the drought recovery assessed on a 5-point scale (Fig. 6). Species were assessed in cover classes in sub-plots measuring 10×1 m. The results are summarised in Table 1 and Figs 7–9. At each site rocks were collected from several excavations of 25 cm cubes of soil. Rock volume was later determined by water displacement.

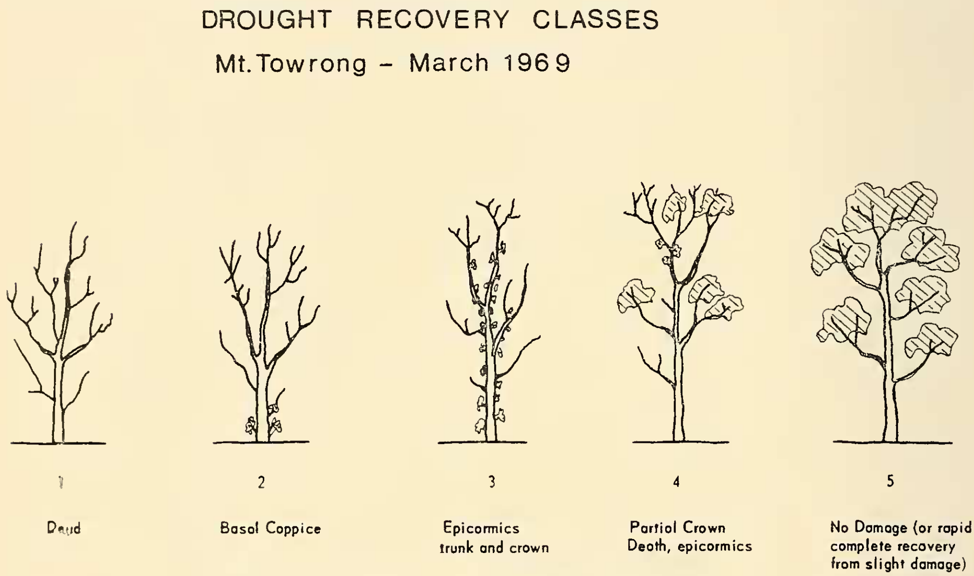

Fig. 6. Drought recovery categories of eucalypts.

Vegetation

The vegetation of the Mount Towrong area varies widely from a fern gully along Stony Creek to a low woodland of almost " mallee " habit on the rockiest sites. Moisture supply appears to be the most important factor controlling vegetation distribution ; hence such features as aspect and slope, the depth and volume of soil, depth to water table and altitude of cloud condensation are likely to be important. The terms used in the description are largely those defined in Leeper (1970). Except where indicated, the nomenclature of species follows that of Willis (1970, 1972).

OPEN FOREST

Wet Sclerophyll Forest Type[1]

This open forest occurs as a ribbon along Stony Creek and on the lower eastern slopes of the Towrong spur. Along the creek mature *Eucalyptus obliqua* and *E. viminalis* reach heights of 27–31 m with occasional *Acacia melanoxylon*

[1] This is a well-entrenched term in Australian ecology ; hence it is proposed to keep it within the framework of formations defined by Specht in Leeper (1970).

TABLE 1

The distribution and cover of major species along the Mount Towrong transect

Aspect	SW–W	SW	Summit	E	Gully and Lower E
Moisture status	Dry		to		wet
Formation	Low grassy woodland	Grassy woodland	Open grassy forest	Open bracken forest	Wet sclerophyll open forest
Associations	*E. goniocalyx* ; *Themeda*	*E. goniocalyx* ; *Poa*	*E. obliqua* ; *Lomandra*	*E. obliqua* ; *Pteridium*	*E. obliqua* ; *E. viminalis* ; *Prostanthera*
No. plots	4	4	4	4	3
Mean tree height (m) . .	10	13	16	25	26
Mean tree basal area (m^2)	0·08	0·14	0·11	0·17	0·26
Mean tree drought score	2·0	4·0	3·5	5·0	4·3
Species (Trees and shrubs)					
Eucalyptus goniocalyx . .	+115	2245	+5		1
Acrotriche serrulata . .	+	11	+++		++1
Acacia dealbata . .		2225	++		+
A. verticillata	+				+1
Casuarina stricta . .	1				
E. radiata		122	+		1
E. obliqua		+	45	+15	+23
E. ovata			1		
E. viminalis				+	+
Prostanthera lasianthos					12
Olearia argophylla . .					++1
Coprosma quadrifida . .					+1
(Monocot. herbs and ferns)					
Cheilanthes tenuifolia . .	+12				
Themeda australis . .	+124				
Stipa hemipogon . .	+13				
Microlaena stipoides . .		3		+	+++

TABLE 1.—*continued*

The distribution and cover of major species along the Mount Towrong transect

Aspect	SW-W	SW	Summit	E	Gully and Lower E
Moisture status	Dry		to		wet
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Associations	*E. gonio-calyx*; *Themeda*	*E. gonio-calyx*; *Poa*	*E. obliqua*; *Lomandra*	*E. obliqua*; *Pteridium*	*E. obliqua*; *E. viminalis*; *Prostanthera*
Poa labillardieri . .	1244	3344	1233	45	234
Danthonia spp. . .	+++1	+++1	4	11	+++
Pteridium esculentum . .		1	+122	+222	+2
Lomandra longifolia . .		++	2223	1	
Echinopogon ovatus . .				+1	+1
Tetrarrhena juncea . .				2	+12
Polystichum proliferum . .				2	1
Adiantum aethiopicum . .					+1
(Dicot. herbs) *Dichondra repens* . .	+1				++
Anagallis arvensis . .		+1			
Senecio linearifolius . .		++1			++
Hydrocotyle hirta . .	+	+2		1	++1
Glycine clandestina . .	+1		+11		++
Oreomyrrhis eriopoda . .	+	+	+1		+
Poranthera microphylla		++3			+
Geranium '*pilosum*' . .		+1	+1	+11	+1
Plantago varia		+11			+1
Viola hederacea . .		+1	+++1	11	+++
Oxalis corniculata . .	++11	++11	++11	1	+1
Clematis aristata . .		++1		2	+11
Acaena anserinifolia . .		+111		12	+1
Stellaria pungens . .		+++2		223	++1
Galium sp.				12	+
Mentha laxiflora . .				1	
Asperula scoparia . .				+2	+1

Cover values assessed as : +(1%), 1(1–5%), 2(5–25%), 3(25–50%), 4(50–70%), 5(70–100%). Species recorded with covers of + *only* were not included.

trees of 15–20 m (Fig. 7). *E. radiata* and *E. goniocalyx* are also present but are chiefly found on the margins of this community. A lateral zonation also occurs in the subordinate vegetation. Within 30 m of the stream broad-leaved notophyll to microphyll shrubs (Webb, 1959) such as *Pomaderris aspera*, *Olearia argophylla*, *O. lirata*, *Hedycarya angustifolia* and *Prostanthera lasianthos* are common with ferns (*Polystichum proliferum*) and wiregrass (*Tetrarrhena juncea*) on the ground.

STONY CREEK

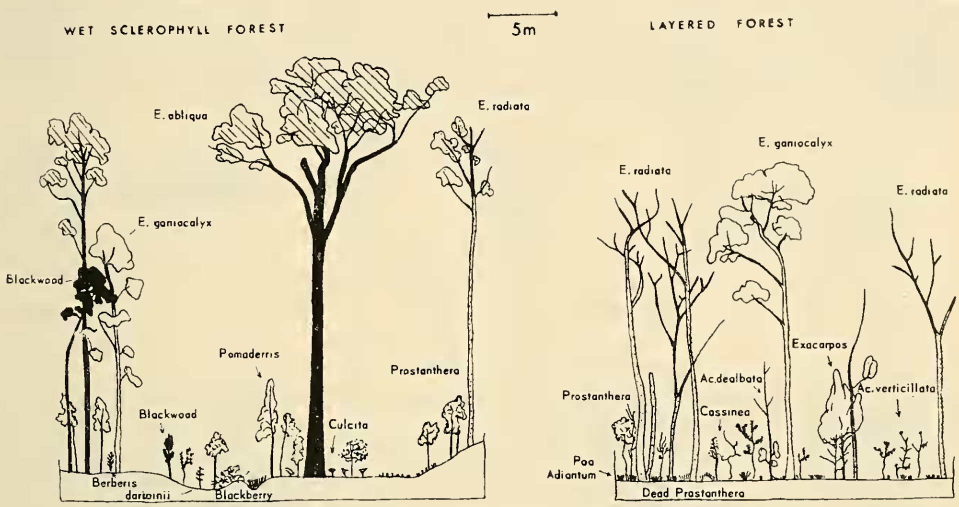

Fig. 7. Vegetation profiles of wet sclerophyll and layered forest.

Between 30 and 60 m from the stream only *Prostanthera lasianthos* and *Olearia lirata* still persist but the undergrowth is dominated by small-leaved shrubs such as *Acacia verticillata* and *Cassinia aculeata* with tussock grass (*Poa labillardieri* Steud.) and maidenhair fern (*Adiantum aethiopicum*) on the ground. The low scrambling shrub, *Bossiaea obcordatum*, is common in the " layered forest " ecotone region between forest and woodland. The nature of this community is likely to be altered in the future due to the great success with which foreign fleshy-fruited species, such as *Arbutus unedo*, *Cotoneaster pannosa* Franch, *Berberis darwinii* and *Rubus fruticosus agg.*, as well as the winged-seeded ubiquitous *Pinus radiata*, have invaded this site from nearby garden estates. On the cool eastern slopes the main forest of *E. obliqua* and *E. viminalis* is an even-aged stand 20–26 m high with mature emergent trees up to 33 m. The woody undergrowth is almost exclusively *Olearia argophylla* with ferns and wiregrass on the floor. The wing-fruited sycamore (*Acer pseudoplanatus*) is actively invading this forest.

Open Grassy-Bracken Forest

This somewhat shorter open-forest occurs on and near the summit of the spur and on the deeper soils of the mid-western aspect. On the upper slopes, where the rockiness of the soil is probably compensated for by the greater incidence of mist, *E. obliqua* dominates a forest of mixed ages up to 15–26 m high. Bracken (*Pteridium esculentum*) is common and is associated with *Poa labillardieri* tussocks and herbs such as *Stellaria flaccida* and *S. pungens*.

On the mid-west aspect the forest consists of mixed ages of *E. radiata* and *E. goniocalyx*. Scattered shrubs occur—*Acacia dealbata* being frequent and *Olearia lirata* quite rare—and the ground stratum consists of the grasses *Poa labillardieri* and *Microlaena stipoides.*

WOODLANDS

Grassy Woodland

These more open stands are 12–18 m high and occur in sites of lower moisture status than that of the forest. They are found in the zone surrounding the forests on the western aspect. On the lower slopes they are dominated by *E. goniocalyx* with some *E. radiata* with a grassy floor of *Poa labillardieri*, *Danthonia* and *Stipa* species. On the upper slopes *E. obliqua* is dominant with a rather unexpected occurrence of swamp gum, *E. ovata*. *E. pauciflora* is found in this community but is very rare. The floor of these stands is covered with tussocks of *Lomandra longifolia* together with *Dianella tasmanica*, *Poa labillardieri* and herbs such as *Stellaria pungens* and *Asperula scoparia* (Fig. 8).

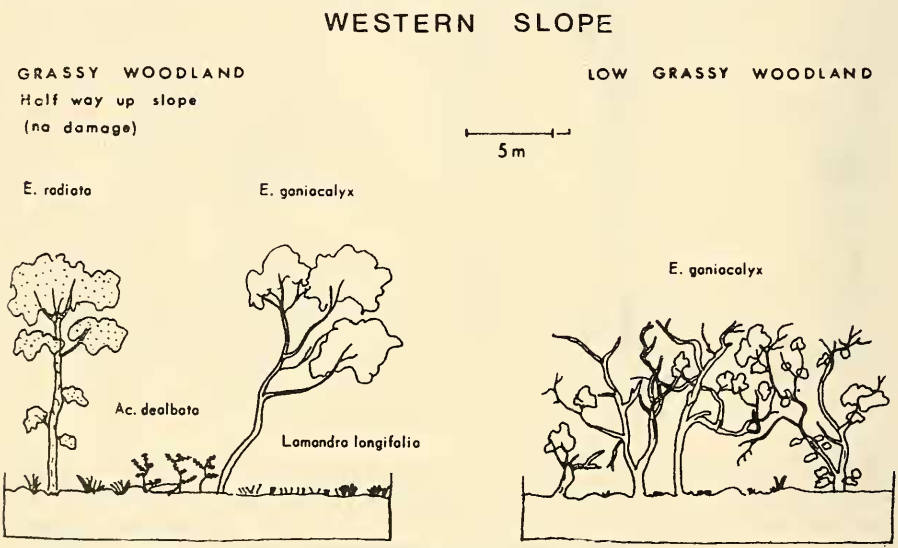

Fig. 8. Woodlands and low woodlands.

Low Grassy Woodland

These relatively open stands occur on the westerly aspects and range in height from 8–11 m. They occur on rocky shallow soils with rock volumes in the upper foot between 25% and 33%; hence drainage and run-off are excessive and the total water storage very low. *E. goniocalyx* is the dominant tree and frequently assumes a twisted mallee-like habit. On the upper slopes the trees are denser although the canopy is sparse. The floor of the stand consists of the grasses *Poa* and *Danthonia* spp. together with occasional low shrubs of *Acrotriche serrulata* and *Bossiaea prostrata*. At lower elevations, where rainfall is lower and amelioration of the climate by fog drip is less frequent, *Casuarina stricta* is often co-dominant (Fig. 9). The floor of these stands is dominated by the grasses *Themeda australis*, *Stipa hemipogon* and *Danthonia* spp. with frequent occurrences of the rock fern, *Cheilanthes tenuifolia*, and the prostrate shrub, *Astroloma humifusum*.

In sites with massive rock outcrops trees are sparse and stunted and the vegetation consists of xerophytic lichens, mosses, rock ferns, grasses and low shrubs in micro-communities which suggest stages of primary succession. The low woodlands follow the north-south trend of the rocky soil across the western aspect and to a limited extent onto the south-western aspect. Sheet erosion is occurring in most of these stands and has possibly been aggravated by the exposure of bare ground during the recent prolonged drought.

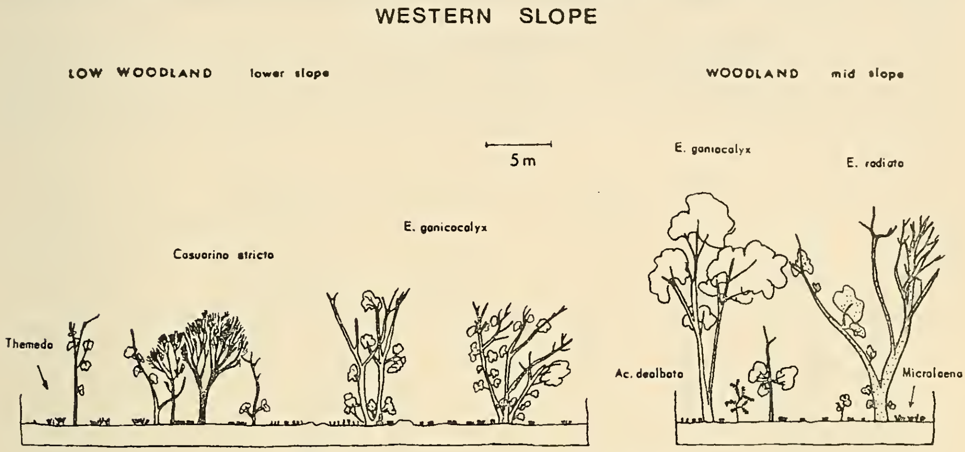

Fig. 9. Woodlands and low woodlands.

The Pattern of Drought Damage

The drought damage of 1967–68 on Mount Towrong was patchy and chiefly confined to the exposed westerly slopes and to the zones marginal to creeks and dry gullies (Fig. 10). No damage occurred on the cooler east and south-east slopes and only occasional damage occurred on the ridge top. Low woodlands were severely damaged on the western aspect below altitudes of about 730 m where rock volumes in the upper 30 cm of soil exceeded 20% but were much less damaged above this level due probably to the modifying effects of low cloud. Damage also occurred in tall woodlands on the mid-western slope and in a belt of tall forest parallel to, and slightly above, Stony Creek.

The forests of the southern, eastern and mid-western slopes were not damaged, due probably either to the greater amount of soil water storage and joint plane seepage at depth or to lower radiation loads. Undamaged forests also occurred on the rocky ridge summits where the low soil moisture could have been compensated by the greater incidence of mist and fog. Trees rooted in rocky soils up to 6 m above Stony Creek were undamaged due to the proximity of the water table to the root zone. Many trees and shrubs between 6 and 18 m above Stony Creek were severely damaged. At 18 m such forest gave way to undamaged woodland. It is likely that in this marginal forest zone the water table and its capillary fringe fell below the root zone of most of the species during the 1967–68 drought. The degree of drought damage of trees tended to increase with density of stems on any given site (Fig. 11). In an area north of the transect line, well spaced mature *E. radiata* trees were little damaged whereas young dense stands nearby were killed or severely damaged. The worst affected stands of *E. goniocalyx* on rocky sites were without exception very stunted and often multi-stemmed. Since fire scars are very rare, the " mallee " habit of these trees is likely to have resulted from dieback of the mainshoot caused by drought. It would appear that the high density of apparently old trees on many of the poor sites is due to the curtailment of height growth and the failure of potentially superior individuals effectively to suppress and eliminate those nearby which are weaker. The partitioning of available water supplies amongst a large number of individuals could result in severe stress, particularly if the leaf area is high and leaf cast is ineffective in sufficiently reducing water demand. The resilience of a species on these sites will depend not only on its inherent resistance to water stress and subsequent regeneration from lignotubers but also on the persistence of such regrowth in spite of such factors as animal browsing, insect attack and fungal

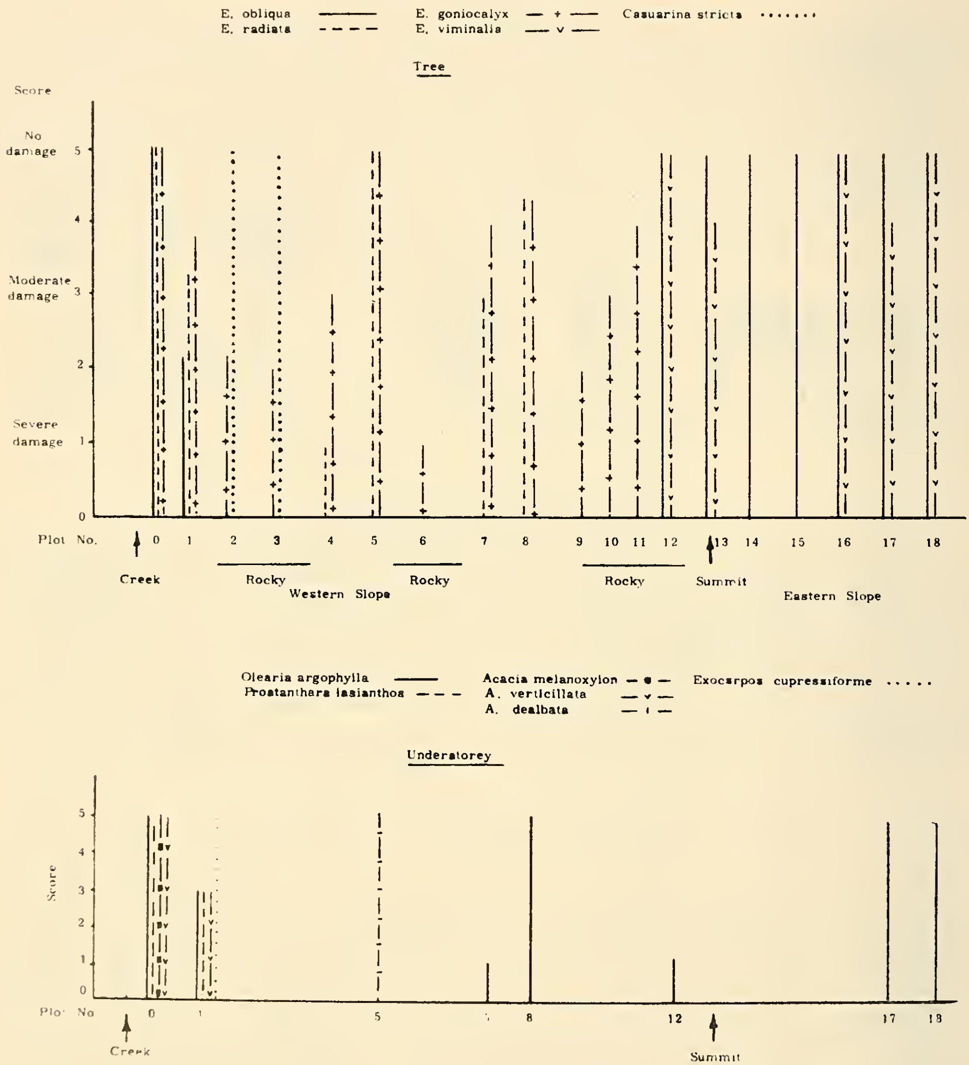

Fig. 10. Drought recovery distribution of trees and shrubs along transect using 0–5 scale (from no recovery to full recovery).

infection. The coppice growth of *E. ovata* one year after the drought, for example, was selectively browsed very heavily, presumably by wallabies. Many trees in the gully coppiced after the drought but succumbed to the fungal parasite, *Armillaria mellea* (Vahl) Fr., in the following year.

There was marked differential drought damage between species on the one site. Such differences have been recently noted by Kirkpatrick (1970) between

E. sideroxylon and *E. bicostata* at Airey's Inlet, Victoria. In general the order of damage was similar to that predicted from the distribution of the species along moisture gradients. *E. goniocalyx* is the most ecologically widespread species in the area and ranges from wet sclerophyll forests along Stony Creek to the hottest and driest sites on north-westerly aspects. In the marginal areas of the wet sclerophyll forests it was much less severely damaged than any of the other eucalypts. In the forest-woodland ecotone on the mid-western slopes *E. radiata* was clearly more severely damaged than was *E. goniocalyx*. In this site *E. radiata* has been able to establish 40–50 m into the woodland area but now could be placed at a competitive disadvantage with *E. goniocalyx* as a result of this exceptional drought. The permanence of this effect will depend on the

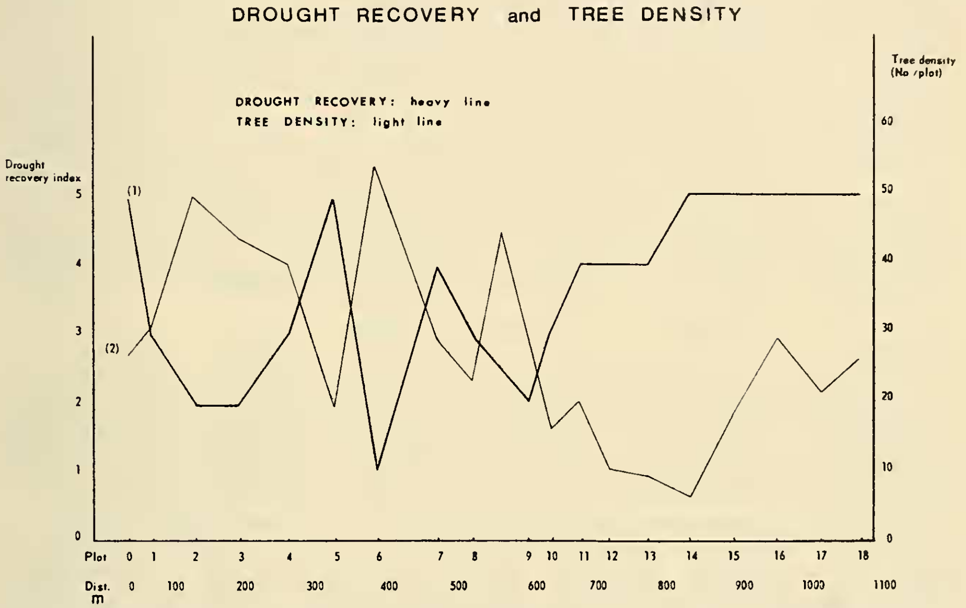

Fig. 11. Relationship between tree recovery and tree density. Line (1) : Drought recovery ; line (2) : Tree density.

frequency of such catastrophes in the life time of the trees. Differential resistance also occurred between understory species. In the Stony Creek forest a lateral gradation of drought damage occurred up the western slope. The most mesic species (e.g. *Pomaderris aspera*) were damaged 1·5–3 m above the creek in sites where little or no damage of *Prostanthera lasianthos* and *Olearia argophylla* occurred. Further above the creek at 12–15 m these latter species and *Olearia lirata* were extensively damaged whilst *Acacia verticillata*, *Exocarpos cupressiformis* and *Cassinia aculeata* were undamaged. On the margin of this forest these species were damaged whilst the low scrambling shrub, *Bossiaea obcordatum*, was undamaged. The latter species however was killed where it had grown out onto the rocky soils of the woodlands on the slope above. A similar understory differentiation occurred in the mid-western slope where *Olearia lirata* was badly damaged in comparison with *Acacia dealbata*. The drought resistance of *Pinus radiata* in a small plantation in the low woodlands on the south-west slope was far superior to that of the surrounding *E. goniocalyx*. The general vigour of the swards of *Themeda australis*, *Stipa hemipogon* and *Cheilanthes tenuifolia* in 1969 suggests that these species were little affected by the drought.

Other patches of forest on the Mount Macedon massif up to the summit at 997 m were also damaged in the drought. On northern catchments *E. obliqua* was observed to have been more damaged than *E. viminalis* in mixed stands (Pl. I, top). In the Mount Towrong area *E. viminalis* was little damaged and was not considered of sufficient importance to be included in the experimental work.

Experimental Work

In order to gain further insight into the relative behaviour of the dominant species on Mount Towrong and their particular distribution in relation to probable moisture gradients, limited experiments on the water relations of seedlings were undertaken. It would have been preferable to have measured the water potentials of tree species and their seedlings during the whole period of the drought and to have referred these to precise measurements of soil moisture and microclimate. The detailed work of Pook *et al.* (1966) shows the efficiency of such an approach. The resistance of the species to drought, whether by endurance or avoidance, would have enabled definitive statements to be made concerning their physiological and ecological adaptations. However, since no such work has been done on these species, the resistance of the plant to wilting treatment, the control of cuticular transpiration, the desiccation of leaf tissues and the resistance to high temperatures were investigated. Since establishment of seedlings is often difficult in dry environments, the development of the initial root system was also investigated. The seed sources were confined to areas within 70 km of Melbourne and ranged from the Brisbane Ranges to Kinglake.

Preliminary Droughting Experiments (1969-70)

Method

It was decided to base these experiments on a recognisable state of the plant in the cycle of desiccation—namely, the permanent wilting point. The length of wilting period, the age and condition of the plant and the environmental conditions throughout will all affect the severity of the symptoms developed. Because of the uncertainty of weather, plants which had been hardened in the open for several weeks were transferred to a well-lit glasshouse for desiccation treatment. The plants all had young growing tips and wilting was easily observed. In the first experiment a dwarf cultivar of sunflower, *Helianthus annuus*, were grown with the test plants to facilitate the recognition of the droughted condition. In general the test plants wilted at about the same time as this standard mesophyte and the permanent wilting condition generally occurred one day after the first signs of tip wilting. The wilting of *Casuarina* was not so obvious but could be recognised by curving of the branchlets and a deepening of the longitudinal furrows. In the first experiment eight replicates of 4 month old seedlings (one per pot) 18–30 cm high were droughted in 15 cm diameter plots of sandy loam under mild sunny conditions in autumn 1969. Different batches were wilted for one and four days after which they were watered and assessed for leaf and axillary bud damage some weeks later.

In the second experiment large lignotuberous plants 18 months old and 0·5–1 m high were grown in two-gallon buckets of sandy loam and allowed to wilt for four days under hot dry glasshouse conditions in late summer 1970. The buckets were heavily insulated from evaporation by Alfoil and daily weighing of pots enabled some estimates of transpiration to be made during the process of desiccation.

Results

In the first experiment, the ranking of species according to their seedling's resistance to glasshouse desiccation was exactly the same as the relative drought resistance observed for trees on Mount Towrong following the 1967–68 drought, viz. *C. stricta*, *E. goniocalyx*, *E. radiata* and *E. obliqua* (Table 2). In all species the younger leaves were the more resistant and in *E. goniocalyx* there was a tendency for stressed leaves readily to absciss and for the stems to show little die-back. In the second experiment the order of drought resistance between species remained much the same. However, one plant of *E. radiata* showed exceptional resistance to drought and failed to wilt and finally turned pale green and became brittle. It was omitted from the assessments since it could not be compared readily with other individuals. The transpiration of the different species varied

TABLE 2

Desiccation damage in preliminary glasshouse experiments 1969–70

	E. obliqua	*E. radiata*	*E. goniocalyx*	*C. stricta*
Expt. 1 May 1961 : 14–19°C, 54–93% R.H.				
Av. height (cm)	26	25	32	18
% damage (leaf and stem) ..				
1 days wilting	7	0	0	0
4 days wilting	63	42	23	14
No. plants/10 killed	1	2	0	0
No. plants/10 undamaged ..	0	1	3	4
Expt. 2 Feb. 1970 : 25–36°C, 40–85% R.H.				
Av. height (cm)	132	99	148	61
Av. leaf area (dm^2)	19·7	18·9	18·1	3·2*
Transpiration at field capacity				
g/day	1138	792	754	462
$g/dm^2/day$	63·3	32·0	42·0	36·3*
% damage after 4 days wilting				
% leaf killed	85·3	90·2	68·8	no leaves
% branch killed	51·3	52·1	9·4	0·9
Lignotuber development (cm)				
Max. width at lignotuber ..	2·1	3·1	3·7	1·6†
Stem width above lignotuber	1·4	1·1	1·5	1·1

* ½ cylinder area.

† carroty swelling

greatly. When water supply was abundant on the first day of the experiment, *E. obliqua* with its large intermediate leaves transpired much faster per unit area than any of the other species. *Casuarina* transpired more slowly and was barely affected by the wilting treatment. The superior drought resistance of the branches of *E. goniocalyx* was again apparent when compared with the other eucalypts.

Droughting Experiments: Assessment of Relative Turgor, Water Potential and Transpiration Rates. December 1971 to January 1972

METHODS

In this major experiment a wilting period of four days was again employed and disc samples were removed from leaves at intervals to assess the changes in relative turgor (=relative water content) (Barrs and Weatherley, 1962). *Casuarina* seedlings were pre-pruned to various levels so that internode samples for relative turgor encompassed a range of branchlet sizes. Eight replicates of seedlings 15–20 cm high were grown in plastic pots of 15 cm diameter in sandy loam. The pots were carefully insulated from direct sunlight by Alfoil and the soil surface covered with 2 cm of white plastic pellets to minimise direct evaporation. Controls proved these measures to be effective. The pots were weighed before sunrise and a control set watered up to their initial field capacity each day. A further set of pots were sown with dwarf sunflowers to check on the uniformity of wilting response. Transpiration of seedlings was expressed per unit leaf area although for *Casuarina* half cylinder area was used. Transpiration of stems was studied by pruning a number of plants of each species to about four leafless branches of about the same diameter range. The cut ends were sealed and the pots insulated and weighed on several consecutive days. The weight loss was expressed per unit surface area.

The relationship between relative turgor and water potential was obtained by allowing cut shoots to dry out for varying lengths of time in the laboratory. The foliage was sampled for relative turgor by floating discs on water for four hours and obtaining fresh and dry weights. Short pieces of shoot were placed in a Scholander pressure bomb and the air pressure necessary to force water from the cut stem recorded. It was thus hoped to infer the kind of internal conditions developed by the seedlings during the wilting treatment.

TABLE 3

Damage and stress of species in major experiment December 1971–January 1972

Damage	*E. obliqua*	*E. radiata*	*E. goniocalyx*	*C. stricta*
Species alone (8 replicates)				
% leaf killed	92·4	32·2	53·7	no leaves
% branch killed	87·4	12·4	2·5	0·7
Wilting score (1–5) ..	5·0	3·7	4·7	4·5
% plants killed	66	12	0	0
In presence of sunflower				
% leaf killed	100·0	100·0	52·7	no leaves
% branch killed	100·0	100·0	1·0	3·0
% plants killed	100·0	100·0	0	0
% sunflowers killed ..	0	0	30·0	0
Relative turgor (%)				
At field capacity	90	89	88	93
At permanent wilting ..	75	70	70	80
After 4 days wilting ..	46	43	38	63
Water potential (–bars)				
At field capacity	10·8	13·4	16·7	10·9
At permanent wilting ..	19·9	24·1	24·4	18·4
After 4 days wilting ..	27·7	36·4	37·5	27·5
Lowest water potential corresponding to 50% damage	24·1	34·1	38·2	not achieved
Water content foliage (% O.D.W.)				
At field capacity	250	260	170	413
At permanent wilting ..	215	228	135	285
After 4 days wilting ..	136	100	84	171
% water content drop/unit water potential from field capacity to wilting point	3·7	3·3	2·2	1·4
Soil moisture (% O.D.W.)				
At field capacity	30·0	30·0	30·0	30·0
After 4 days wilting ..	6·8	5·4	5·0	5·1

RESULTS

The ranking of the seedlings according to severity of damage was again much the same as that in the preliminary experiments (Table 2). *C. stricta* was extremely resistant and *E. obliqua* extremely susceptible to the stress imposed by wilting for four days in average diurnal temperature ranging from 16–29°C. Many *E. obliqua* plants were killed whereas only some of the finer branchlets of *C. stricta* died. The damage to *E. radiata* and *E. goniocalyx* was intermediate in severity. In this experiment *E. radiata* foliage was less damaged and the stems more damaged than those of *E. goniocalyx*. The population of *E. radiata* proved very variable—some plants died rapidly whilst others wilted only slightly and remained grey-green and resistant for a relatively long time. The onset of wilting of all the species was not greatly dissimilar from that of the sunflowers. The rapid loss of water caused by the additional leaf area of the sunflowers caused a dramatic increase in the death rate in *E. radiata* seedlings (Table 3 ; Fig. 12). The extremely mesophytic sunflowers largely recovered from their severely wilted condition.

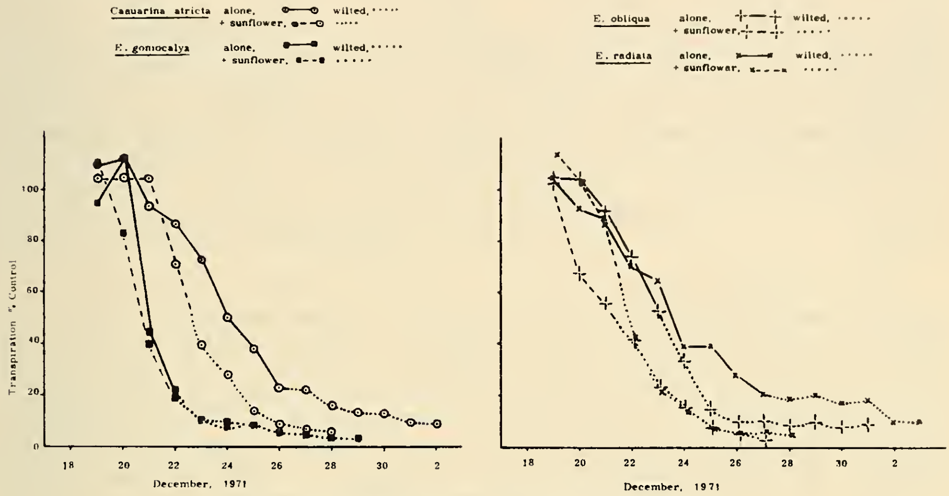

Fig. 12 Transpiration during wilting experiment.

The larger plants of *E. goniocalyx* depleted their moisture supply at the fastest rate of any species ; however, on the basis of water loss per unit area at field capacity, *E. goniocalyx* transpired less than the other eucalypts (Table 4). No plants of this species were killed. *E. obliqua* tended to transpire faster per unit area than any of the other species (Fig. 13). The average time taken for plants to reach wilting point was shorter in *E. goniocalyx* and *E. obliqua* than in *E. radiata* and *C. stricta*.

TABLE 4

Transpiration rates during major experiment 1971–72

	E. obliqua	*E. radiata*	*E. goniocalyx*	*C. stricta*
Mean height (cm)	37	28	61	54
Leaf area (dm²)	2·48	2·77	7·31	2·31(4·62)*
Transpiration (g/dm²/day)				
Controls 11 day average ..	20·5	19·1	17·0	30·4 (15·2)*
Desiccating plants				
initial rate (wet)	29·0	23·6	19·5	23·7 (11·8)*
after 10 days (dry) ..	2·1	4·8	0·7	4·2 (2·1)*
Branch transpiration (2–4 mm diam.)				
g/cm²	0·50	0·64	0·32	0·97
Transpiration control plants				
Alone (g/day)	74·4	66·5	143·0	69·6
+Sunflowers (g/day) ..	134·0	125·5	153·5	91·8
Av. no. days taken to reach wilting point (range in brackets)				
Tree seedlings	5·0	8·4	4·2	7·1
	(3–8)	(4–16)	(3–6)	(4–9)
Tree seedlings+Sunflowers ..	3·6	3·2	3·4	4·6
	(3–5)	(3–4)	(3–5)	(3–5)

* *Casuarina* : calculated on ½ cylinder and (full cylinder) basis.

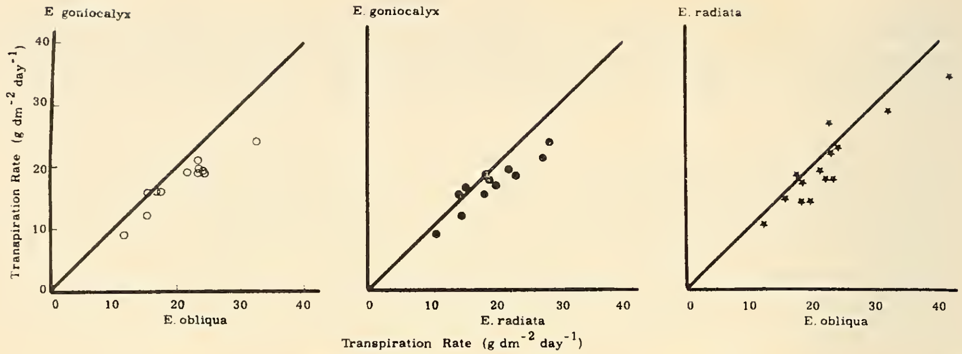

Fig. 13. Comparative transpiration of species at or near full turgor. Diagonal line indicates equal rates.

The relationship between relative turgor and water potential (Fig. 14), although variable, is similar for *E. goniocalyx*, *E. radiata* and *C. stricta*. *E. obliqua* does not reach the correspondingly low water potentials of the other species. During desiccation certain similarities and differences were apparent in water relations in these species. *E. obliqua*, which was so readily damaged, showed similar trends to *C. stricta*, which was hardly affected by the treatment. Both *E. obliqua* and *C. stricta* develop a similar range of relatively low water potentials on wilting, although *C. stricta* has a much higher moisture content throughout (Table 3). Likewise *E. radiata* and *E. goniocalyx* develop a similar

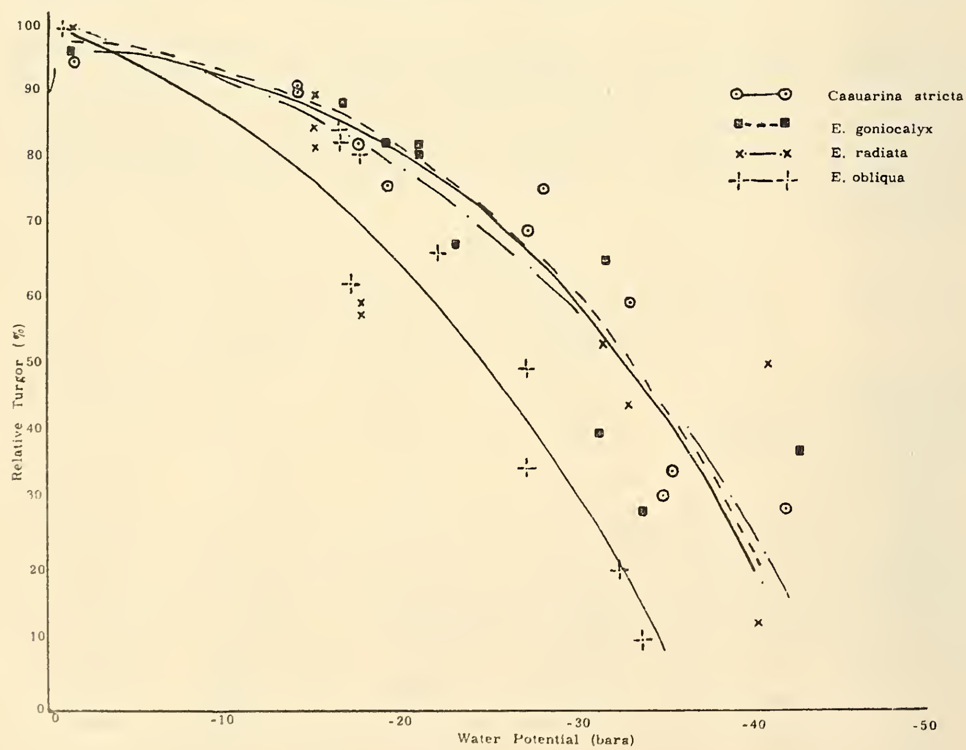

Fig. 14. Relationship between relative turgor and water potential.

range of relatively low water potentials during desiccation. The moisture content of *E. goniocalyx* is relatively low throughout and the relative transpiration rates per unit area for foliage and stems is markedly less than *E. radiata*.

Detached-leaf Dehydration

METHOD

In these experiments tree foliage was obtained from Mount Towrong and juvenile foliage from glasshouse seedlings hardened outside for more than one month (Fig. 15). The aim of the experiment was to investigate any differential cuticular control of water loss when stomata had closed. Twenty replicates of leaves were placed at random on 1 cm mesh wire netting in the laboratory in January 1972 for up to 20 hours. The temperature was 28°C and relative humidity 72%. Batches of leaves were weighed at intervals, their relative turgor determined and any damage due to desiccation assessed. Water potentials were derived from the relationship shown in Fig. 14.

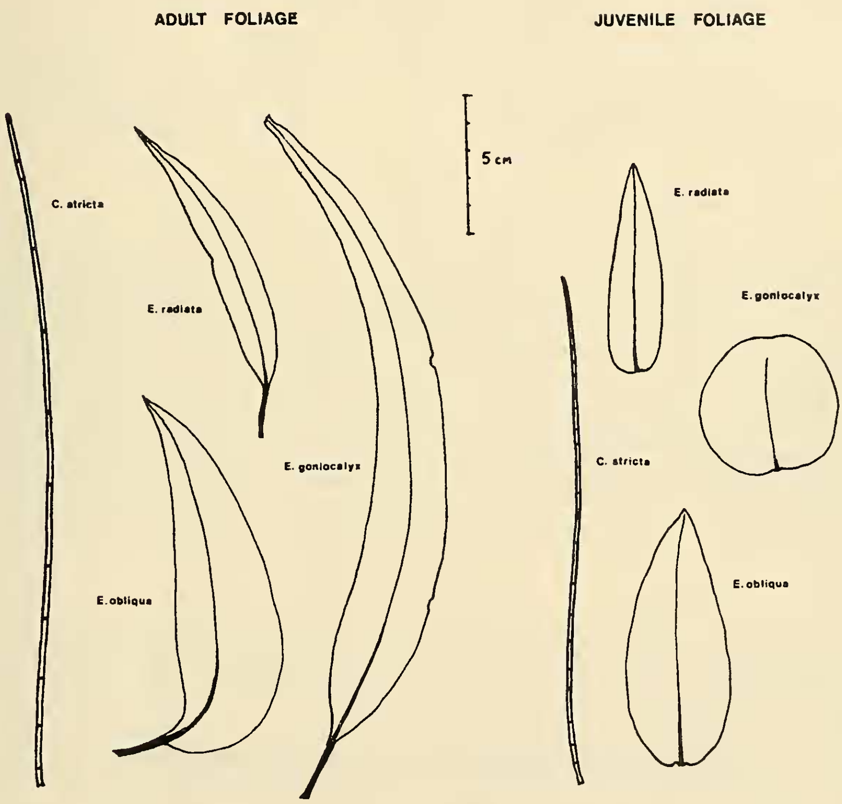

Fig. 15. Juvenile and adult foliage of the test species.

RESULTS

The results of relative moisture loss from juvenile leaves showed a general similarity to the relative rates of transpiration of glasshouse seedlings. Both adult and juvenile leaves of *E. obliqua* lost water rapidly during their stomatal transpiration phase and developed low water potentials. Severe damage occurred after only five hours. Juvenile and adult *E. goniocalyx* and juvenile *E. radiata* leaves controlled water loss efficiently by early stomatal closure and significant damage did not occur until 20 hours of drying. *C. stricta* was extremely efficient at preventing water loss and it would appear that stomata shut early in the drying treatment. It was quite undamaged after 20 hours drying. It also possessed an initially high water content and owing to the slight water loss did not develop low water potentials.

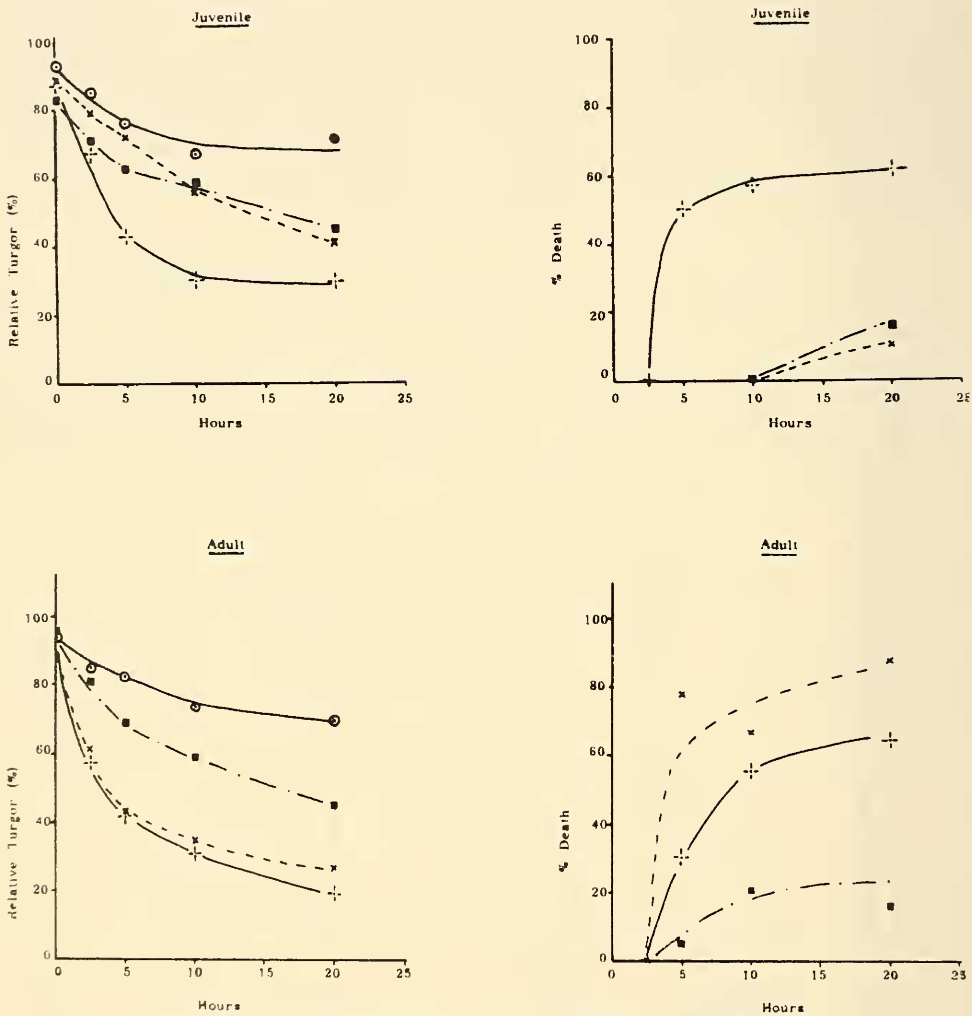

Fig. 16. Relative turgor and death of drying detached leaves.
⊙ = *C. stricta* ; + = *E. obliqua* ; × = *E. radiata* ; ■ = *E. goniocalyx*.

A most marked difference in behaviour occurred between the adult and juvenile foliage of *E. radiata* (Fig. 16). The adult foliage lost water rapidly and was severely damaged and was thus similar to both types of *E. obliqua* foliage. The juvenile foliage on the other hand behaved similarly to *E. goniocalyx*. The behaviour of adult and juvenile leaves of the other species did not differ greatly. The cuticle thickness of the juvenile foliage showed only slight differences— *E. goniocalyx* being the thinnest (5–6 μm) and *E. radiata* and *C. stricta* the thickest (7–9 μm). However, the relative order of cuticle thickness of the adult foliage was reversed—*E. goniocalyx* being the thickest (9–18 μm) and *E. radiata* the thinnest (6–9 μm). The cuticle of the longitudinal ridges of *C. stricta* was thicker (9–12 μm) than that of the grooves (3–5 μm). The mass of thickened hairs, which arise amongst the stomata in the grooves and extend up to 75 μm beyond the cladode periphery, are likely to increase the depth of the boundary layer and thus minimise transpiration rates (Slatyer, 1964). The " needle " form of the cladode could also increase the rate of heat dissipation and lead to a better conservation of water by this species (Slatyer, 1967). The relative sclerophylly, as expressed by area per unit dry weight of foliage, differs between the four species studied. It also increases from juvenile to adult foliage and the amount of increase is roughly in the order of the drought resistance of the species.

Table 5

Foliage area/dry weight ratios (cm^2/g)
(The half cylinder area calculated for Casuarina*)*

	E. obliqua	*E. radiata*	*E. goniocalyx*	*C. stricta*
Juvenile ..	92·5	110·2	100·3	67·7
Adult ..	64·4	70·9	53·7	37·7
Juvenile/adult	1·46	1·56	1·87	1·80

Tissue Resistance of Juvenile Leaves to Dehydration

Method

In order to assess the relative resistance of the foliar tissues to different degrees of desiccation, discs were suspended on a small mesh cradle above 20 ml of H_2SO_4 so as to produce relative humidities of 99%, 98%, 97%, 96% and 95%. A somewhat similar method was used by Weatherley and Slatyer (1957) to determine the relationship of diffusion pressure deficit and relative turgor. The phials used were as small as practicable. Ten 7 mm discs were cut by cork borer from the eucalypt leaves and 15 internode segments were cut from *Casuarina* using a sharp razor. The samples were weighed daily until equilibrium had been obtained in 4–5 days. The experiment was carried out at 25°C under a light intensity of 1000 lx. The relative turgor was assessed and the percentage of area damaged was noted for each species.

Results

The results suggested that the order of resistance to desiccation was similar to that obtained from other experiments, although there was a tendency for the species to pair into two groups—the more " mesophytic " *E. obliqua* and *E. radiata* and the more " xerophytic " *E. goniocalyx* and *C. stricta*. It is apparent that the former two species were more damaged by slight reductions in relative humidity and that the damage increased rapidly with decrease in water potential. The latter two species develop low water potentials without appreciable damage up to a critical level beyond which damage increases very rapidly indeed (Fig. 17). A water potential of −30 bars in leaf tissues causes 100% death of *E. obliqua*, 40% death of *E. radiata* and 1–5% of *E. goniocalyx* and *C. stricta*. The water potential necessary to kill 50% of the area is −28 bars for *E. obliqua*, −34 bars for *E. radiata*, −37 bars for *E. goniocalyx* and −40 bars for *C. stricta*. These values are fairly close to those obtained during the wilting experiments (Table 2) although for *Casuarina* such water potentials were never reached under the conditions of glasshouse wilting.

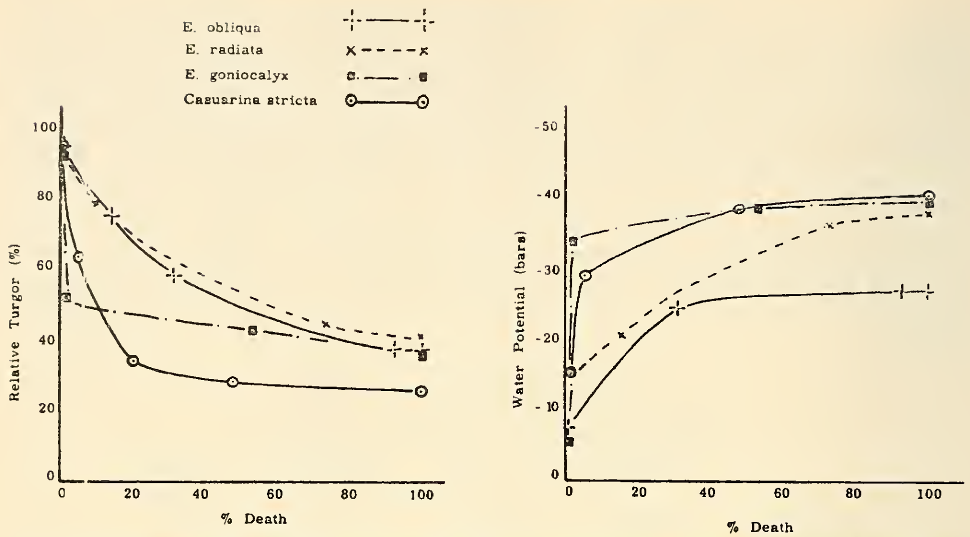

Fig. 17. Death of tissue in equilibrium with various relative humidities. Relative humidities were produced by equilibrium with aqueous solutions of H_2SO_4.

Leaf Temperatures and Heat Resistance

Methods

Henckel (1964) showed that overheating of leaves during desiccation in bright sunlight could be a factor contributing to drought damage. The relative temperatures of turgid and wilted leaves of each species were measured in the glasshouse during the major experiment (1971–72). A thermocouple needle was held firmly against the leaf surface away from the direct sunlight. Only leaves facing the sun at an angle of less than 10° and greater than 75° to the horizontal were investigated.

The relative resistance of leaves to wet heat was briefly investigated by plunging them into controlled well-stirred water baths at different temperatures for two minutes. Longer times were avoided in order to minimise the possibility of water penetration into the leaves. In one experiment, wilted leaves were sheathed in thin plastic sheeting prior to immersion. The damage sustained was qualitatively assessed after 24–48 hours (Table 6).

Results

As expected, the temperatures of leaves in still, warm, sunny conditions were markedly affected by both their moisture status and the orientation of their laminas to the direct sunlight. Turgid, transpiring leaves developed temperatures 3–6°C higher than ambient under these conditions. However wilting leaves developed temperatures 6–14°C greater than ambient. Horizontal leaves were as much as 6°C warmer than vertical or near vertical leaves. Thus *E. goniocalyx* developed high leaf temperatures because most of the sessile orbicular juvenile leaf remains horizontal on wilting. Most of the wilted foliage of *E. obliqua* and *E. radiata* hangs vertically and therefore avoids much of the excessive heat of midday. If *E. goniocalyx* juvenile leaves had not been glaucous it is likely that their temperatures would have been much higher.

The effect of hot water immersion of the foliage suggests that *E. obliqua* juvenile leaves were more sensitive than the other eucalypts and that *Casuarina* was the most resistant of the four species studied. In general, the tree adult foliage was more sensitive than the juvenile, particularly that of *E. radiata* and

Table 6

(a) Leaf temperatures °C, 24.12.71. Glasshouse experiment

Leaf orientation	Plant watered		Plant wilted	
	Horizontal	Vertical	Horizontal	Vertical
E. obliqua	33·3	30·2	38·4	32·8
E. radiata	30·2	30·2	36·4	35·0
E. goniocalyx	32·2	29·2	38·5	32·4
C. stricta				
diam. 1 mm	28·3		30·0	
2 mm	30·2		34·0	

Ambient temperature 26·5°C, ventilating breeze 0·2 m/sec.

(b) The relative heat tolerance of leaves. Preliminary experiment

Water temperature (°C)	% Leaf damage to seedling (a) and tree (b)							
	E. obliqua		*E. radiata*		*E. goniocalyx*		*C. stricta*	
	(a)	(b)	(a)	(b)	(a)	(b)	(a)	(b)
50	0	0	0	0	0	0	0	0
55	45	16	36	12	38	30	0	4
60	92	75	44	80	60	100	30±	35
65	100	100	100	100	100	100	80	100
70	100	100	100	100	100	100	100	100
Leaf thickness and cladode diam. (mm)	0·27	0·27	0·21	0·20	0·28	0·35	1·12	1·26

E. goniocalyx. Heating wilted leaves in closely appressed thin plastic sheaths considerably increased the damage sustained; however, the relative order of species' susceptibility was not greatly altered.

The Development of Seedling Root Systems

Method

It is clear that the depth and extent of the root systems of the various species at different stages of their development need to be known before any work on the mechanisms of drought avoidance can be assessed (Johnson *et al.*, 1968).

Table 7

Comparative root and shoot growth. Glasshouse trials 1969–72

	E. obliqua	*E. radiata*	*E. goniocalyx*	*C. stricta*
1. *Two weeks old*				
Autumn 1969				
Root depth (cm)	2·8	1·8	5·3	6·6
2. *Four weeks old*				
Spring 1971				
Root depth (cm)	21·5	18·3	29·4	32·1
Shoot height (cm)	1·7	1·7	3·2	10·5
No. leaves	2·0	2·0	3·6	3·3*
Root/shoot	12·6	10·8	9·2	3·1
3. *Twelve weeks old*				
Summer 1972				
Root D. wt. (g)	0·089	0·069	0·140	0·189
Shoot D. wt. (g)	0·140	0·070	0·102	0·201
Root/shoot	0·64	0·99	1·37	0·94

* branchlets.

Such laborious field work was beyond the scope of the present study. However, the early development of the root and shoot may permit valuable inferences to be made about the likely success of seedling establishment in the environment of the seed source (Toumey and Korstian, 1947 ; Zimmer and Grose, 1958). Seeds were sown in large pots or plastic pipes (10 × 100 cm) containing either sandy loam or krasnozem soil. Three experiments were set up at different times from winter to summer from 1969 to 1972.

Results

The results set out in Table 7 clearly show consistent relative differences in behaviour of the species. *C. stricta* produced the longest tap root and heaviest root system in the first few weeks of growth, probably due to the fact that this species has by far the largest seed weight. Of the eucalypts, *E. goniocalyx* consistently produced the largest tap root and the heaviest total root weight. Both *E. obliqua* and *E. radiata* were relatively slow to produce a sizeable tap root and those of *E. obliqua* were slightly longer than those of *E. radiata*, a feature which may have reflected the slightly heavier seed.

Discussion

The study of the distribution of damage amongst the various species on Mount Towrong has shown that the vegetation on both the hot dry slopes with shallow soils and the gully margins with deeper soil was the worst affected. The pattern is therefore similar to that described for New South Wales and the Australian Capital Territory in 1965 by Pook *et al.* (1966). From an examination of the relative damage of trees and shrubs in the various ecotones between different vegetation types, the species could be ranked in order of their relative drought resistance.

The severe damage along creeks could be attributed to the development of a large demand for water under a normally reliable regime. It is probable that the water table was lowered beyond the reach of roots in this zone and hence dramatic damage occurred in these communities. The severe damage to the low vegetation on the worst hot and rocky sites could not be attributed to a lower resistance on the part of the dominant *E. goniocalyx* but rather to its being the only species capable of enduring such recurrent stress. *C. stricta*, which characteristically occupies such sites, only occurs on the lower slopes and was virtually undamaged. Its restricted distribution on Mount Towrong could be due to the proximity of its upper altitudinal limit in this area. The ranking of the species according to their relative drought damage in the field is compatible with general ecological observations on their broader relationships to moisture gradients in southern Victoria.

The glasshouse and laboratory experiments, although artificial and dealing mainly with seedlings, point to several possible mechanisms by which these dominant species have become adapted to their several well-circumscribed sites. When seedlings of these dominant species are allowed to wilt for various times the amount of damage they sustain is directly proportional to the order of their ranking of field drought resistance.

From every point of view *C. stricta* seems to be the best adapted species to drought stresses. This highly xerophytic plant is able to avoid desiccation for long periods by efficient stomatal and cuticular control of water loss. With good water supply its transpiration per unit area is high on a half cylinder basis but low on a total surface area basis. Water loss is curtailed at relatively high relative turgors and high water potentials. The tissues have a high water content, possibly due to the core of central parenchymatous pith. However, the contribution of cell wall water to the water balance of the leaf (Carr and Gaff, 1962) may prove to be important in this xeromorphic species. When its " cladode " tissues are dehydrated they endure more stress than the more mesophytic eucalypts. In the wilting experiments of seedlings, its conservation of tissue water was so efficient that the limit of endurance was never reached. The development of a rapidly descending tap root would be an undoubted advantage in dry sites where excessive evaporation from the surface soil takes place.

Conversely, *E. obliqua* was the most mesophytic species studied. Its transpiration rates per unit leaf area were higher than the other eucalypts and only moderate water potentials were developed with the onset of dehydration. The water content of the foliage was reduced to a low level and tissues were incapable of withstanding much stress. The great majority of plants died following sustained wilting. Detached leaves, both juvenile and adult, rapidly lose water and appear to have little stomatal and cuticular control of water loss. If this behaviour occurs in the field it would allow rapid loss of water supplies and continued dehydration of tissues early in the drought period, thus minimising its chances of survival. Moreover, the leaves are large, relatively poor dispersers of heat and appear fairly susceptible to high temperatures. The relatively slow descent of the seedling tap root would be a disadvantage to establishment on dry sites.

The other two species, *E. goniocalyx* and *E. radiata*, appear to have different strategies for survival under dry conditions. *E. goniocalyx* is the most conspicuously dimorphic species studied. The waxy glaucous seedling has the ability to control transpiration during the onset of desiccation and cuticular transpiration is low. The general water content of the foliage is relatively low and the plant develops low water potential under prolonged stress. The tissues appear to be able to withstand a relatively high stress and then, like those of *C. stricta*, suddenly succumb. It is apparently not as efficient as *C. stricta* in avoiding drought but it has the capacity readily to shed older stressed leaves, thereby reducing its transpirational load. In spite of their high reflectivity, wilted leaves may heat up considerably under high radiation due to the maintenance of a horizontal orientation. The leaves, however, appear to have a relatively high heat resistance. The long leathery adult leaves are also efficient controllers of cuticular water loss but appear to be more sensitive to high temperatures. *E. radiata* also has markedly dimorphic foliage and was the most physiologically variable species in this study. Some seedlings were mesophytic and, like those of *E. obliqua*, transpired rapidly and died. Others were like those of *C. stricta* and controlled transpiration efficiently, hardened and occasionally resisted desiccation for a long time. This ability by some individuals to regulate water use was completely negated by the association of a wastefully transpiring mesophyte such as the dwarf sunflower. Under these conditions all the seedlings of *E. radiata* died. The ecological implication from such an observation could be that the behaviour of a species to drought in pure stands could be very different from its behaviour in a mixed community, especially if important associated species had different regimes of water use. The juvenile leaves were much more efficient in controlling cuticular transpiration than the adult leaves and were more resistant to experimental desiccation. If such characteristics occur in the field it is possible that the seedlings of this species may be more drought resistant than the tree. However, the early establishment of the seedling in dry sites is likely to be jeopardised by the very tardy development of the root system. This particular feature could differentiate between otherwise equally resistant genotypes of *E. radiata* and *E. goniocalyx*.

In general these studies support the conclusions of Jarvis and Jarvis (1963*a* and *b*), in that the most drought resistant tree species are often those which respond quickly to small changes in relative turgor, close stomata and avoid further water loss by efficient cuticular control. Sanchez-Diaz and Kramer (1971) have stated that more drought resistant species permit less reduction of water content for a given reduction of water potential. In support of this idea, the water content loss per unit decrease in water potential for the Mount Towrong species form a graded series compatible with all aspects concerned with their relative drought resistance. Quraishi and Kramer (1970) found that seedlings of eucalypt species derived from flood plain environments are less drought resistant than those from rocky hillsides and that the ability to avoid drought stress by stomatal control was of great importance. Grieve and Hellmuth (1970) stressed the importance of diversity of adaptation in Western Australian sclerophyll species and the drought escape by the development of deep root systems was a significant feature of some species such as *E. marginata*. Lamb and Florence (1973) have pointed out the subtleties that exist between the local distribution of some eucalypts, such as *E. robertsonii* and *E. fastigata*, and physical features of the soils, such as total moisture storage, pore space and the acceptance of light summer showers.

Hopkins (1964) has shown that the growth rate of eucalypt seedlings could be a crucially important factor in survival in habitats prone to drought. Fast growing species in rich soils in such environments require a correspondingly large moisture supply to meet their demands. Thus *E. regnans* may die if it is encouraged to outgrow the ability of the site to supply sufficient moisture. Parsons (1968) likewise stressed the importance of slow growth rates as a survival mechanism in mallee species in southern Australia. The Mount Towrong observations are analogous to those made by Martin and Specht (1962) in the Mount Lofty Ranges, South Australia. Their studies showed that the soil moisture was depleted faster under the more mesophytic *E. obliqua* forest on southerly slopes than was that under the more xerophytic *E. goniocalyx* forest on the hot northerly slopes. They suggest that tree seedlings and understory species in the *E. obliqua* forest may in fact suffer more prolonged water stress than those in the *E. goniocalyx* woodlands on a warmer slope. It is possible that a similar situation could occur on Mount Towrong. The total leaf area on the eastern aspects certainly appears to be greater than that on the western aspects and experiments suggest that there is an inherent tendency for *E. obliqua* to transpire faster than *E. goniocalyx* on a leaf area basis. However, the local climate attending the development of water stress on these contrasting aspects could be decisive in dictating the degree of damage inflicted. The cool eastern slopes may permit a diurnal replenishment of moisture supply above the lethal limit, whereas the hot western slopes may be subjected to increasingly severe stress due to the high air and soil temperatures and the impact of hot dry winds that blow from that quarter. It is clear that the tolerance limits of *E. goniocalyx* have been reached in shallow soils on this aspect. It is notable that the ligno-tuber of seedlings is much better developed in *E. goniocalyx* than in *E. obliqua*, a feature that could be important in aiding survival on droughted sites (Table 2).

The ecological distribution of the dominants on Mount Towrong suggests a response to two general modes of the environment; the average or median conditions and the rare extremes. A species may spread along a moisture gradient on to dry sites in periods of adequate rainfall and then be eliminated or greatly reduced in importance by the occurrence of rare extreme drought. Thus *E. radiata* has spread up to 50 m beyond its " safe " limit on the western aspect of Mount Towrong where it has been severely damaged. As has been pointed out by Jones (1945) the frequency of catastrophes or favourable periods within the life span of the tree is of great importance. It is probable that such testing of species distribution has gone on for thousands of years. The ability of a species to develop ecotypes and thus increase its distributional range may well depend on catastrophes which eliminate competing species.

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EXPLANATION OF PLATE

Plate I

Top. Dead *E. obliqua* and living *E. viminalis* on shallow soils, north slopes of Mount Macedon.

Bottom. Mount Towrong from Upper Macedon showing drought damaged areas 60 km north-west of Melbourne.